

Species Diversity, 2006, 11, 7–32

Two New Genera and Species of Ophiuroid (Echinodermata) from Hydrothermal Vents in the East Pacific

Sabine Stöhr¹ and Michel Segonzac²

¹ Swedish Museum of Natural History, Department of Invertebrate Zoology,
Frescativ. 40, Box 50007, 10405 Stockholm, Sweden
E-mail: sabine.stohr@nrm.se

² IFREMER, Centre de Brest, DEEP/Laboratoire Environnement profond-Centob,
BP 70, 29280 Plouzané, France
E-mail: Michel.Segonzac@ifremer.fr

(Received 4 July 2005; Accepted 15 November 2005)

Prior to this study, two species of ophiuroid had been described from hydrothermal vent sites, and another from methane cold seeps, all from the Atlantic Ocean. Although ophiuroids have occasionally been reported from vents in the Pacific Ocean as well, none has been described before. This study presents two new species, *Spinophiura jolliveti* gen. et sp. nov., family Ophiuridae, and *Ophiolamina eprae* gen. et sp. nov., family Ophiacanthidae, which are most likely endemic to reducing environments in the East Pacific. We also include detailed descriptions of the post-metamorphic development of these species. *Spinophiura jolliveti* is characterized by up to five rather long, semi-erect arm spines and a relatively small oral shield. Its postlarva is unusual in lacking a buccal scale and in that the tooth forms later in development than in all other species the postlarvae of which have been examined. The most characteristic features of *O. eprae* are the attitude of the three proximal laminar mouth papillae, standing almost vertically on the oral plate, and the presence of two oval, scale-like, distal papillae. Additional migrant (non-vent-endemic) species found at Pacific vent sites are tabularized, but not identified below genus level due to the poor taxonomic state of the Pacific ophiuroid fauna. Biogeographic and ecological issues are discussed.

Key Words: Brittle stars, postlarval development, Ophiuridae, Ophiacanthidae, SEM, morphology, taxonomy, hydrothermal vent, cold seep.

Introduction

Deep-sea hydrothermal vents are found along all mid-ocean ridges and form an ecosystem based on bacterial chemosynthesis (Van Dover 2002). Vents have been studied intensively since their discovery in 1977 and they harbour a unique invertebrate fauna with specific adaptations to the thermal and chemical conditions that prevail there (Tyler *et al.* 2003). Similar ecosystems are found at methane cold seeps and around whale skeletons. Despite the fact that echinoderms dominate the errant megafauna on the deep-sea floor (Gage and Tyler 1991), few species occur at hydrothermal vents and seeps, and none has yet been found on whale skeletons (Smith *et al.* 2002). Ophiuroids were largely unknown in these environments until

recently. Hecker (1985) reported ophiuroids from cold seeps, but they remain undescribed. A decade ago, the first vent- or seep-inhabiting ophiuroid species, *Ophiectenella acies* Tyler *et al.*, 1995, was described from the TAG (Trans-Atlantic Geotraverse), Snake Pit, and Broken Spur vent fields on the Mid-Atlantic Ridge (MAR) (Tyler *et al.* 1995). Since then, *Ophiactis tyleri* Stöhr and Segonzac, 2005 has been described from the Menez Gwen vent field on the MAR, but it remains to be seen whether this species is restricted to vent localities, and *Ophienigma spinilimbatum* Stöhr and Segonzac, 2005 has been found at seeps in the Gulf of Mexico and is likely endemic to these sites (Stöhr and Segonzac 2005). Ophiuroids have been reported occasionally from vent sites in the Pacific Ocean (Sibuet and Olu 1998; Halanych *et al.* 1999), but none has been described. Describing new species from the Pacific Ocean is problematic, because the ophiuroid fauna of the Pacific is not as well-studied as that of the Atlantic Ocean. The literature is scattered, difficult to access, often outdated, and occasionally employs multiple names for the same morphological species. A first attempt at revising part of the Pacific ophiuroid fauna resulted in a large number of synonymisations and the description of several new species (O'Hara and Stöhr in press).

In this paper we report on the ophiuroids found at hydrothermal vents and cold seeps on the East Pacific Rise (EPR; Fig. 1), Easter Microplate, and Pacific-Antarctic Ridge, and in the Manus Back-Arc Basin (N off Papua New Guinea) and Nankai Trough (SW Japan), and describe the first two species of ophiuroid endemic to vent environments in the Pacific. The material includes individuals of different ontogenetic stages and thus allows the analysis and detailed description of the post-metamorphic development of both species. Juveniles have been described for probably no more than 50 species of ophiuroid (Stöhr 2005 and literature cited therein) and additional data are important for understanding the phylogenetic relationships between taxa. Accurate descriptions of juveniles may also serve as a tool for ecologists, since most identification keys are based on adult characters.

Materials and Methods

During several different cruises (Table 1), ophiuroids were collected by using a slurp gun, a scoop, or a grab from submersibles and remotely operated vehicles (ROV). An exception to this were the samples collected by the SEPR (South East Pacific Rise) cruise under supervision of C. Van Dover using the manned submersible *Alvin* (Table 1). On that cruise a quantitative collecting method was employed featuring specially designed pots, which reduced the loss of associated organisms (Van Dover, pers. comm.).

Samples were washed, preserved in formalin, and later transferred to 80% ethanol. Selected specimens were submerged in household bleach (NaOCl diluted with water 1:1) for 10 to 30 seconds, depending on the size of the specimen, to remove the epidermis and expose the skeleton. Skeletal elements were prepared by treating a specimen with undiluted household bleach until all soft tissues had disappeared. The specimens were then washed in water, dried, and mounted on aluminium stubs for scanning electron microscopy (SEM). As adhesive, a non-permanent spray glue was used. Small specimens were mounted wet on the glue and left

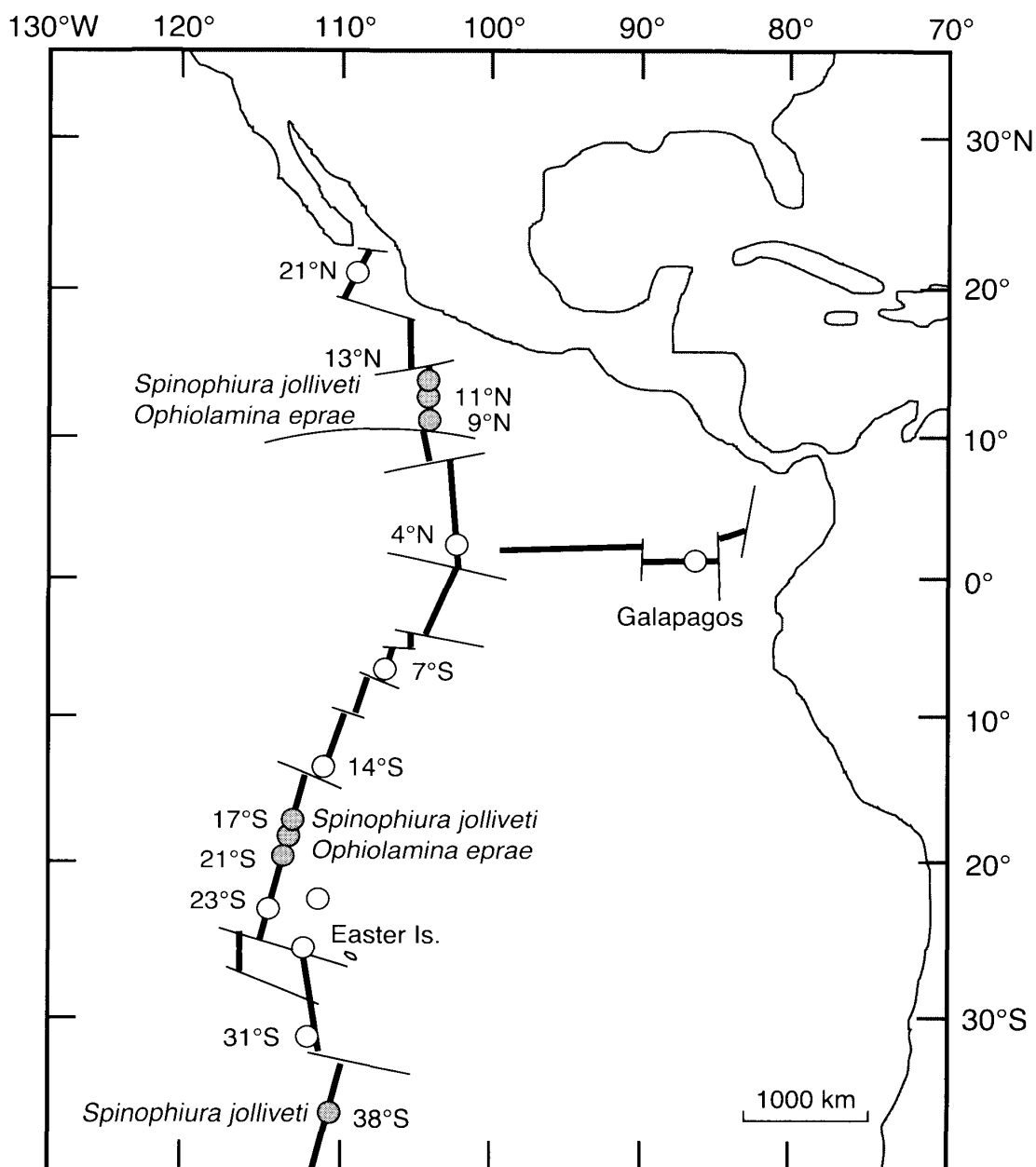


Fig. 1. Hydrothermal vent sites on the East Pacific Rise and Pacific-Antarctic Ridge. Full circles mark the vent sites where one or both of the new species of ophiuroids, *Spinophiura jolliveti* and *Ophiolamina eprae*, were collected. See Table 2 for details.

to dry. To scan both sides of an animal, most of the glue was dissolved in butyl acetate and its residue brushed off, and then the specimen was remounted with fresh glue. The glue could not always be completely removed from small specimens due to the risk of damage from the mechanical stress of the fine brush. After coating with gold, the specimens were examined with a Hitachi FE-4300 SEM. Size measurements were taken off the instrument's scale bar or, with large specimens, by using a dissecting microscope fitted with an ocular micrometer. The size of a specimen (spm) is given as disk diameter (dd).

Table 1. Cruises to the Pacific Ocean during which the ophiuroids described in this paper were collected.

Cruise	Chief Scientist	Ships/ROVs	Region	Date
KAIKO-NANKAI	X. Le Pichon, ENS, Paris	NO <i>Nadir</i> / DSV <i>Nautil</i>	Nankai Trough, SW Japan	13/08– 09/09/1989
HERO 91	D. Desbruyères, Ifremer, Brest	NO <i>Nadir</i> and RV <i>Vickers</i>	EPR, 13°N, 9°50'N	30/09– 04/11/1991
PITO	J. Francheteau, UBO, Brest	NO <i>Nadir</i> / DSV <i>Nautil</i>	Easter Microplate	11/1993
NAUDUR	J.-M. Auzende, IRD, New Caledonia	NO <i>Nadir</i> / DSV <i>Nautil</i>	EPR, N of Easter Island	03– 30/12/1993
NAUTIMATE	B. Mercier de Lépinay and F. Michaud, Université Nice, France	NO <i>Nadir</i> / DSV <i>Nautil</i>	off Mexico	16/01– 09/02/1994
HOT 96	F. Gaill, Université Paris VI	NO <i>Nadir</i> / DSV <i>Nautil</i>	EPR, 13°N, 9°N	09/02– 23/03/1996
BIOACCESS 98	J. Hashimoto, JAMSTEC, Japan	NO <i>Natsushima</i> / DSV <i>Shinkai 2000</i>	SW Pacific, Manus Basin, N of Papua New Guinea	13– 25/11/1998
SEPR	C. L. Van Dover, Williamsburg, U.S.A.	DSV <i>Alvin</i>	SEPR, 17°S	02/02– 23/02/1999
HOPE 99	F. Lallier, Roscoff, France	NO <i>Atalante</i> / DSV <i>Nautil</i>	EPR, 13°N, 9°N	09/04– 25/05/1999
PHARE	N. Le Bris, Ifremer, Brest	NO <i>Atalante</i> / ROV <i>Victor 6000</i>	EPR, 13°N	30/04– 03/06/2002
FIELD	J. Voight, Penn State University	DSV <i>Alvin</i>	EPR, 9°N	10– 12/11/2003
BIOSPEEDO	D. Jollivet, CNRS, Roscoff	NO <i>Atalante</i> / DSV <i>Nautil</i>	EPR, 07°–21°S	31/03– 13/05/2004
PAR 5	R. Vrijenhoek, MBARI, California	RV <i>Atlantis</i> / DVS <i>Alvin</i>	PAR, 23°–38°S	12/03– 06/04/2005

Regional abbreviations: EPR, East Pacific Rise; PAR, Pacific-Antarctic Ridge; SEPR, South East Pacific Rise.

Juveniles were matched to adults of the same species by tracing skeletal characters backwards through the growth series, a method successfully applied in previous studies (Sumida *et al.* 1998; Stöhr 2005). The terminology used follows Sumida *et al.* (1998) and the classification follows Smith *et al.* (1995). Type material has been deposited at the Swedish Museum of Natural History, Stockholm (SMNH); the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); and the Muséum National d'Histoire Naturelle, Paris (MNHN), as indi-

cated below. All non-type material has also been deposited at the MNHN.

Results

All specimens of ophiuroids found on the EPR belong to two families, Ophiuridae and Ophiacanthidae (Table 2). The most abundant species (270 individuals) is new to science and described below as *Spinophiura jolliveti* gen. et sp. nov. (Fig. 2), family Ophiuridae. The post-metamorphic development of the species is described in detail (Figs 3, 4). The second most common species (31 individuals) is described below as *Ophiolamina eprae* gen. et sp. nov., family Ophiacanthidae (Fig. 6). A growth series of this species was also available to use in describing its postmetamorphic development (Figs 7, 8). Neither of these species has so far been found in non-reducing environments. The species found at the Nankai Trough cold seep sites and other species at vents, of which single or few individuals were found, are most likely bathyal species and belong to the families Ophiuridae and Ophiacanthidae. These species are documented in Table 2 for later reference.

Spinophiura jolliveti and *Ophiolamina eprae* have been found sympatrically at four vent sites in roughly the same area between 17°25'S and 18°36'S (Table 2). *Ophiolamina eprae* was also found at 12°48'N (type locality), but not between this locality and the southern area. *Spinophiura jolliveti* was found between 9°N and 38°S. Both species are absent at the Manus Basin vent field and are probably restricted to the EPR. Farther to the north and south, single specimens of other species were found.

Taxonomic Account

Family **Ophiuridae** Lyman
Genus ***Spinophiura*** gen. nov.

Diagnosis. The genus reaches a dd of up to 10 mm. Distinct arm combs continue across the arm base. There are up to five semi-erect arm spines, which are longer than an arm joint. The mouth papillae are spine-like, numbering 10–14 to one side of a jaw. The first tentacle pore in the mouth slit bears one to three spine-like papillae. The oral shield is just over a third as long as the ventral disk. The up to seven tentacle scales are spine-like.

Etymology. The genus name is composed of *spin(a)* from Latin for “spine”, and *Ophiura*, to indicate its affinities with that genus; gender feminine.

Type species. *Spinophiura jolliveti* sp. nov.

Description. As for type species.

Spinophiura jolliveti sp. nov.
(Figs 2–4, 5A–C)

Holotype. 10 mm dd, dry, MNHN EcOs 22635.

Type locality. Cruise HOPE 99, *Nautila*, dive PL 1372, 3 May 1999, EPR-9°N,

Table 2. Collecting sites of ophiuroids at hydrothermal vents and cold seeps in the Pacific Ocean.

Site	Dive	Equipment	Latitude	Longitude	Depth (m)	Species	N	Env
Nankai Trough	KN05	Box core	33°49.80'N	137°55.20'E	1999	<i>Ophiomitrella</i> sp.	1	CS
Nankai Trough	KN06	Box core	33°50.00'N	137°49.70'E	2153	<i>Ophiomitrella</i> sp.	2	CS
Nankai Trough	KN09	Box core	33°47.80'N	137°49.70'E	2095	<i>Ophiomusium</i> sp.	1	CS
Nankai Trough	KN14	Box core	33°49.40'N	137°55.20'E	2060	<i>Ophiomusium</i> sp., <i>Ophiomitrella</i> sp.	1, 1	CS
EPR, 9N, East Wall	HE09	Basket 1	09°50.99'N	104°17.59'W	2491	<i>Spinophiura jolliveti</i>	1	V
EPR, 9N	HE614	Basket	09°40.30'N	104°17.50'W	2520	<i>Spinophiura jolliveti</i>	1	V
Easter Microplaque, Terevaka Fault	PI19-15		24°17.35'S	115°37.35'W	1830	<i>Ophiacantha richeri?</i>	1	CS?
SEPR, Rehu	ND06-2		17°24.85'S	113°12.15'W	2580	<i>Spinophiura jolliveti</i> , <i>Ophiacantha</i> sp.	14, 1	V
SEPR, Animal Farm	ND12		18°36.50'S	113°23.98'W	2673	<i>Spinophiura jolliveti</i>	1	V
Off Mexico	NM10-4	Basket	18°22.00'N	104°22.98'W	3259	<i>Ophiura</i> sp.	23	CS
EPR 9N, Biovent	HT1073	Basket 2	09°50.78'N	104°17.61'W	2532	<i>Spinophiura jolliveti</i>	2	V
EPR 9N, Biovent	HT1078	Basket 1	09°50.78'N	104°17.61'W	2532	<i>Spinophiura jolliveti</i> postlarvae	2	V
EPR, 13N, Parigo	HT1090	Basket 1	12°48.25'N	103°56.34'W	2648	<i>Spinophiura jolliveti</i>	1	V
BAB Pacmanus, Field E	BA1075		03°43.65'S	151°40.41'E	1694	<i>Amphiura</i> sp.	1	
SEPR, Animal Farm	A3343, A3349	Samples 1, 2, 4, 5	18°36.43'S	113°23.96'W	2675	<i>Ophiolamina eprae</i> , <i>Spinophiura jolliveti</i>	16, 3	V
SEPR, Oasis	A3358	Sample B-6	17°25.40'S	113°12.32'W	2582	<i>Spinophiura jolliveti</i>	1	V
EPR, 9N, East Wall	A3489	Pots 2, 4, 5	09°50.53'N	104°17.52'W	2491	<i>Spinophiura jolliveti</i>	6	V
EPR, 9N, Biovent	A3490	Grey box, Pot 6	09°50.99'N	104°17.59'W	2491	<i>Spinophiura jolliveti</i>	3	V
EPR, 9N, East Wall	A3727	Pots 2, 4	09°50.99'N	104°17.59'W	2491	<i>Ophiura</i> sp., <i>Ophiolamina eprae</i>	1, 1	V
EPR, 9N, Train Station	A3728	Biobox 2	09°49.64'N	104°17.37'W	2495	<i>Ophiura</i> sp.	1	V

Table 2. Continued

Site	Dive	Equipment	Latitude	Longitude	Depth (m)	Species	N	Env
EPR, 9N, Mussel Bed	A3740	Pot 1	09°50.57'N	104°17.49'W	2491	<i>Spinophiura jolliveti</i>	1	V
EPR 9N, Biovent	HO1372	Slurp gun 1	09°50.52'N	104°17.62'W	2518	<i>Spinophiura jolliveti</i>	4	V
EPR 9N, Biovent	HO1372	Slurp gun 2	09°50.44'N	104°17.65'W	2518	<i>Spinophiura jolliveti</i>	1	V
EPR 9N, Biovent	HO1375	Basket 4	09°50.50'N	104°17.54'W	2516	<i>Spinophiura jolliveti</i>	3	V
EPR 9N, Mussel Bed	HO1377	Basket	09°50.37'N	104°17.48'W	2512	<i>Spinophiura jolliveti</i>	1	V
EPR 13N, Genesis	HO1386	Basket 4	12°47.72'N	103°55.91'W	2632	<i>Spinophiura jolliveti</i>	5	V
EPR, 13N, PP52	PH155	Slurp gun 2	12°48.69'N	103°56.36'W	2592	<i>Ophiolamina eprae</i>	6	V
EPR, 13N, PP-Ph08	PH164	Slurp gun 4	12°49.01'N	103°56.58'W	2622	<i>Spinophiura jolliveti</i>	1	V
EPR, 13N, PP-Ph08	PH167	Basket	12°49.08'N	103°56.56'W	2621	<i>Spinophiura jolliveti</i>	1	V
EPR, 9N, Tica	A3929, A3931	Artificial substrate	09°50.45'N	104°17.49'W	2500	<i>Spinophiura jolliveti</i>	6	V
SEPR, White Christmas	BS1571	Slurp gun 1	07°23.16'S	107°47.06'W	2735	<i>Ophiura</i> sp.	2	V
SEPR, Oasis	BS1579	Basket 1	17°25.38'S	113°12.29'W	2586	<i>Ophiolamina eprae</i>	1	V
SEPR, Oasis	BS1583	Basket	17°25.39'S	113°12.28'W	2585	<i>Spinophiura jolliveti</i>	15	V
SEPR, Animal Farm	BS1585	Basket 1	18°36.52'S	113°23.99'W	2585	<i>Spinophiura jolliveti</i> , <i>Ophiolamina eprae</i>	132, 5	V
SEPR, Wormwood	BS1587	Basket	17°34.91'S	113°14.67'W	2596	<i>Spinophiura jolliveti</i>	1	V
SEPR, Rehu	BS1590	Basket, Alvinette	17°24.98'S	113°12.14'W	2583	<i>Spinophiura jolliveti</i> , <i>Ophiolamina eprae</i>	51, 2	V
SEPR-PAR	#4091	Scoop	37°40.35'S	110°52.68'W	2232	<i>Spinophiura jolliveti</i>	13	V

Dive numbers are preceded by cruise or vessel name to connect this table to table 1. Abbreviations: A, *Alvin*; BA, BIOACCESS 98; BAB, Back Arc Basin; BS, BIOSPEEDO; CS, cold-seep; Env, environment; EPR, East Pacific Rise; HE, HERO91; HO, HOPE 99; HT, HOT 96; KN, KAIKO-NANKAI; N, number of specimens; ND, NAUDUR; NM, NAUTIMATE; PAR, Pacific-Antarctic Ridge; PH, PHARE; PI, PITO; SEPR, South EPR; V, vent..

hydrothermal vent site Biovent, 09°50.52'N, 104°17.62'W, 2518 m.

Paratypes. For all station data see Table 2. Growth series of 20 spms mounted on SEM stubs and gold-coated: 13 spms, BIOSPEEDO, PL 1585, 26 Apr. 2004, SMNH-

Type-6052–6059, 6076; 7 spms, BIOSPEEDO, PL1590, 1 May 2004, SMNH-Type-6060–6066. Dried samples: 4 spms, BIOSPEEDO, PL 1585, basket 1, 26 Apr. 2004, MNHN EcOs 22636. Samples in ethanol (80% unless stated otherwise): 1 spm, SEPR, dive 3343, Sample 1, 2 Feb. 1999, USNM 1078905; 2 spms, SEPR, dive 3349, 8 Feb. 1999, USNM 1078906; 1 spm, SEPR, dive 3358, Sample B-6, 19 Feb. 1999, USNM 1078907; 3 spms, SEPR, dive 3489, Pot 4, 17 Nov. 1999, USNM 1078908; 1 spm, SEPR, dive 3489, Pot 5, 17 Nov. 1999, USNM 1078909; 1 spm, SEPR, dive 3489, Pot 2, 17 Nov. 1999, USNM 1078910; 2 spms (1 small postlarva, 1 adult), SEPR, dive 3490, Grey box, 18 Nov. 1999, USNM 1078911; 1 spm, SEPR, dive 3490, Pot 6, 18 Nov. 1999, USNM 1078912; 1 spm, SEPR, dive 3740, 26 Dec. 2001, USNM 1078913; 13 spms, PAR 5, dive 4091, 25 Mar. 2005, USNM 1078914; 1 spm, PAR 5, dive 4094, 28 Mar. 2005, USNM 1078915; 3 spms, 95% ethanol, BIOSPEEDO, PL 1583, basket 1, 23 Apr. 2004, MNHN EcOh 20000; 12 spms, BIOSPEEDO, PL 1583, basket 1, 23 Apr. 2004, MNHN EcOh 20001; 7 spms, 95% ethanol, BIOSPEEDO, PL 1585, basket 1, 26 Apr. 2004, MNHN EcOh 20002; 5 spms, 95% ethanol, BIOSPEEDO, PL 1585, BC4, 26 Apr. 2004, MNHN EcOh 20003; 103 spms, BIOSPEEDO, PL 1585, basket 1, 26 Apr. 2004, MNHN EcOh 20004; 1 spm, BIOSPEEDO, PL 1587, basket 1, 28 Apr. 2004, MNHN EcOh 20005; 1 spm, BIOSPEEDO, PL 1590, “Alvinette” box, 1 May 2004, MNHN EcOh 20006; 3 spms, HOPE 99, PL 1372, slurp gun 1, 3 May 1999, MNHN EcOh 20007; 1 spm, HOPE 99, PL 1372, slurp gun 2, 3 May 1999, MNHN EcOh 20008; 3 spms, HOPE 99, PL 1375, basket 4, 6 May 1999, MNHN EcOh 20009; 1 spm (postlarva), HOPE 99, PL 1377, basket, 8 May 1999, MNHN EcOh 20010; 14 spms, NAUDUR, ND06-2, 11 Dec. 1993, MNHN EcOh 20011; 1 spm, NAUDUR, ND12, 17 Dec. 1993, MNHN EcOs 20012; 2 spms, HOT 96, PL1073, basket 2, 25 Feb. 1996, MNHN EcOh 20013; 2 spms (postlarvae), HOT 96, PL1078, basket 1, 7 Mar. 1996, MNHN EcOh 20014; 1 spm, HOT 96, PL 1090, basket 1, 20 Mar. 1996, MNHN EcOh 20015; 1 spm, PHARE, PL167, basket 1, 29 May 2002, MNHN EcOh20016; 1 spm, PHARE, PL 164, slurp gun 4, 25 May 2002, MNHN EcOh 20017; 1 spm, Hero 91, PL 614, 13 Oct. 1991, MNHN EcOh 20018; 5 spms, HOPE 99, PL 1386, 7 May 1999, SMNH-Type-6106; 42 spms, BIOSPEEDO, PL 1590, 1 May 2004, SMNH-Type-6107.

Diagnosis. As for generic diagnosis.

Etymology. The species is named in honour of Didier Jollivet for his accomplishments in studying hydrothermal vent communities.

Description of holotype. The disk measures 10 mm in diameter, and arm length is about 50 mm. The arms rapidly taper, and are whip-like and curled (Fig. 2A). The dorsal disk is formed by numerous round, overlapping scales, among which the primary plates are not obvious. The radial shields are a little longer than wide, their length being about one sixth of *dd*, and they are partly covered proximally by scales; pairs are separated by a wedge-like plate except at their distal ends (Fig. 2C). Below each radial shield there is a distinct arm comb, which continues across the arm. Part of the distal end of the genital plate is visible beneath the radial plate with which it articulates. The comb papillae are pointed, flat, and spine-like. The arm is inserted into the disk with a short incision between the radial plates. The first dorsal arm plate is much smaller than the following plates and is partly covered by the disk, bearing a few short papillae. Each lateral arm plate bears four to five flat, pointed, slightly rugose spines, which are slightly longer than an arm joint. Distalwards the spines become increasingly thorny, and the distalmost spines are curved with a thorny inner edge. The dorsal arm plates are con-

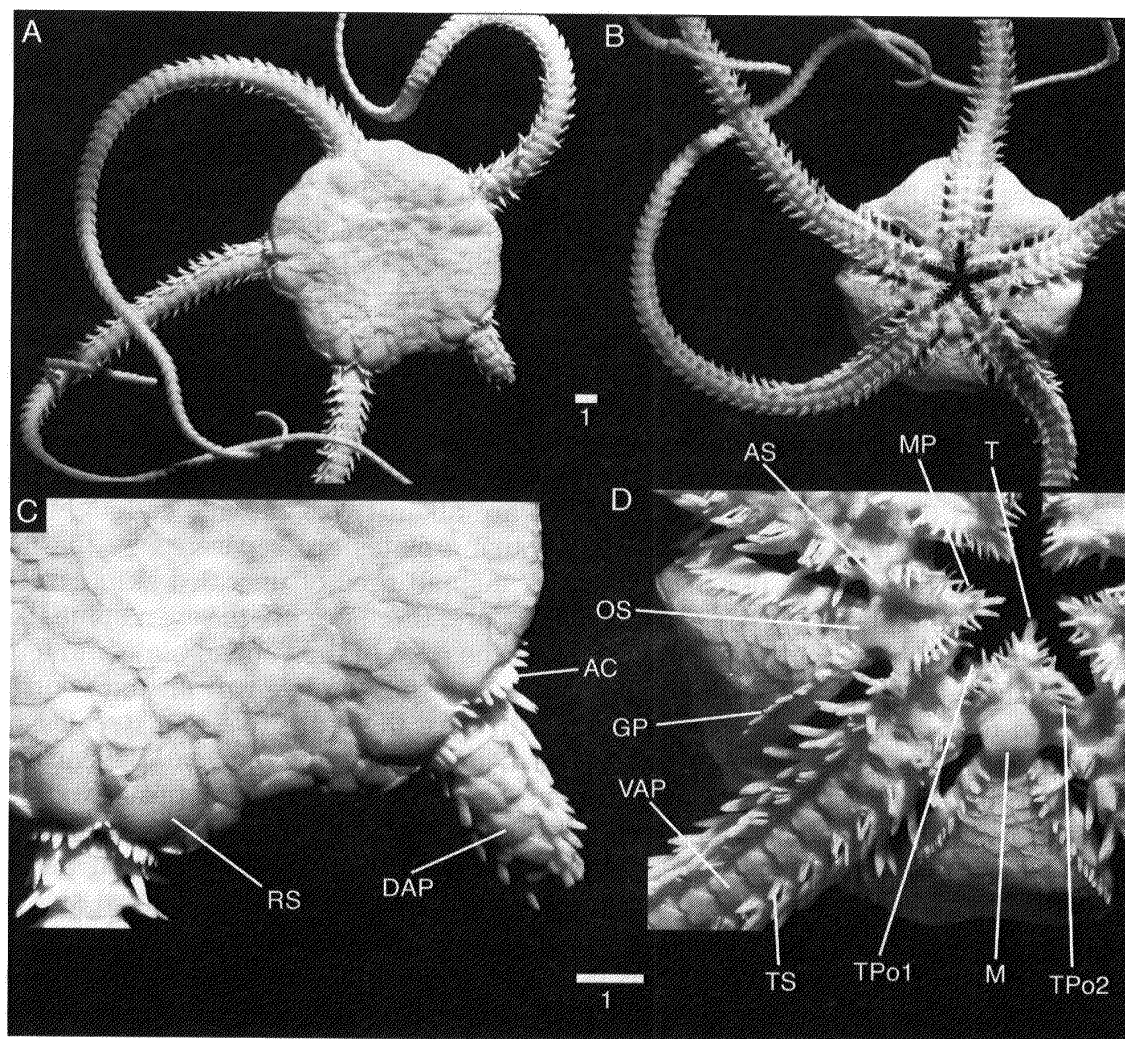


Fig. 2. Holotype of *Spinophiura jolliveti* gen. et sp. nov., MNHN EcOs 22635. A, Dorsal aspect; B, ventral aspect; C, close-up of dorsal disk, showing radial shields and arm combs; D, close-up of ventral disk, showing small oral shield and genital papillae. Abbreviations: AC, arm comb; AS, adoral shield; DAP, dorsal arm plate; GP, genital papillae; M, madreporite; MP, mouth papillae; OS, oral shield; RS, radial shield; T, tooth; TPo, tentacle pore; TS, tentacle scale; VAP, ventral arm plate. Scale bars in millimetres.

tiguous and trapezoidal, with a convex distal edge, their greatest width being about equal to their length.

The ventral disk is formed by small, round, overlapping scales (Fig. 2B). The bursal slit is lined along its proximal half with round, overlapping scales, along its distal half with a long genital scale, which extends around the arm and articulates with the radial shield. On the outer edges of these scales and plate, a row of pointed genital papillae runs from the edge of the oral shield to the dorsal side (Fig. 2D), where it forms the arm comb. The dental plate bears six teeth. There are 10–14 long, slender and pointed, spine-like papillae to either side of a jaw, three of them on the dental plate, three to four on the oral plate, and four to seven on the edge of the adoral shield. Inside the mouth slit on the vertical side of the oral plate at the

edge of the first tentacle pore, one to three slightly smaller but otherwise similar spine-like papillae stand out. The second tentacle pore is superficial and covered by the mouth papillae and additional similar papillae, two to three on the first lateral arm plate and one to two on the first ventral arm plate. The oral shield is shaped like a short arrow, about as long as its greatest width, and at 1 mm it is just a little over a third as long as the interrarial ventral disk (Fig. 2D). One oral shield is larger than the others, swollen and with less pronounced lateral angles, and bearing a pore on the lateral edge next to the bursal slit (not visible in image); this is the madreporite. The adoral shields are narrow and curve around the lateral angles of the oral shield. The first lateral arm plate curves vertically into the mouth angle so that only its distal edge bearing the papillae is visible next to the second tentacle pore.

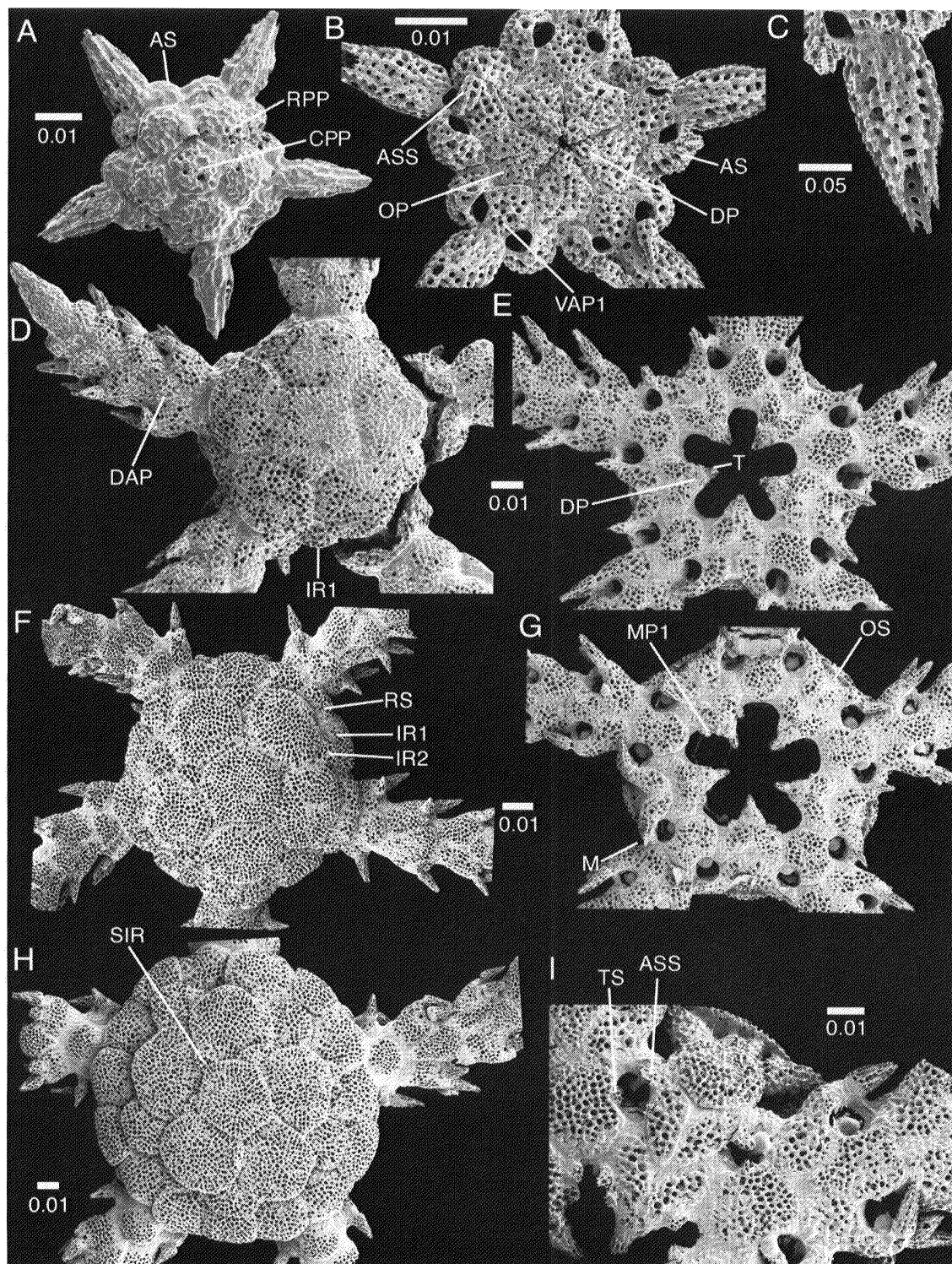
The first ventral arm plate is depressed in its centre and its proximal edge is turned down into the mouth slit. It is smaller than the following plates. On the proximal part of the arm, the ventral plates are about twice as wide as long, with concave proximal and distal edges. Neighbouring plates are separated by the lateral arm plates, which do not meet. Instead, a small area of unscaled skin can be seen between the plates. At the third tentacle pore, there are six to seven spine-like scales, similar to the mouth papillae, three on the edge of the ventral plate and four on the lateral plate. The fourth tentacle pore bears six scales, two on the ventral plate and four on the lateral plate. At the fifth pore there are five to six scales, at the sixth pore five scales; numbers decrease distalwards along the arm. Beyond the disk margin, the ventral arm plates become pentagonal, with an obtuse proximal angle, a concave or notched distal edge, and inward-slanting lower lateral edges. On the distal part of the arm, the ventral plates are longer than wide and neighbouring plates almost meet. The lateral arm plates extend onto the ventral side of the arm along the proximal edge of the ventral plate, but do not meet.

The live coloration of this species is a light beige to cream. The majority of the specimens collected were smaller than the holotype, which is one of the largest adults.

Paratype variation. Only two specimens are as large as the holotype, and those are morphologically similar to the latter. Many of the paratypes of 8–9 mm dd lack the cluster of papillae on the first arm plate connecting both combs. In any single animal, considerable variation exists in the number of mouth papillae between different jaws, as is described above for the holotype. Differences between individuals of different size are due to differences in ontogenetic stage as is explained below.

Post-metamorphic development (paratypes). The smallest postlarva found

Fig. 3. Growth series of *Spinophiura jolliveti* gen. et sp. nov., SEM images, paratypes. A–C, Postlarva of 0.4 mm dd, SMNH-Type-6062, dorsal aspect (A), ventral aspect, demonstrating absence of tooth and buccal scale (B), and terminal plate (C); D, E, postlarva of 0.8 mm dd, SMNH-Type-6076, dorsal aspect (D) and ventral aspect (E); F, G, postlarva of 1 mm dd, SMNH-Type-6058, dorsal aspect (F) and ventral aspect (G); H, I, postlarva of 1.3 mm dd, SMNH-Type-6058, dorsal aspect (H) and ventral aspect (I). Abbreviations as in Fig. 2 plus: ASS, adoral shield spine; CPP, central primary plate; DP, dental plate; IR, interrarial plate; OP, oral plate; RPP, radial primary plate; SIR, secondary interrarial plate. Scale bars in millimetres. Type catalogue numbers refer to SEM stubs, not individuals.



measures 0.4 mm in dd, with arms consisting only of the terminal plate. The dorsal disk is formed by the central primary plate and five radial primary plates, all with an irregular meshwork of fenestrations, multilayered in the centre and single-layered on the margin (Fig. 3A). The bulging first lateral arm plates (=adoral shields) are visible beyond the disk margin at the base of each terminal plate. No oral shields or madreporite are present. The jaws are formed by the two oral plates and the dental plate, which does not bear a tooth (Fig. 3B). The first ventral arm plate is arrow-shaped and flanked by large tentacle pores. The adoral shields each bear a short, tapered spine with minute thorns along its edges. The terminal plate has ribs bearing minute thorns along its length and ends in a ventral opening and several terminal thorns (Fig. 3C).

At 0.8 mm dd and four arm joints in addition to the terminal plate, the dorsal disk is formed by the primary plates and small interradial plates (Fig. 3D). The radial shields have just begun to form distal to the radial primary plates, and the proximal arm joint bears a small, triangular dorsal plate. A minute tooth has formed on the dental plate and the oral shields are just visible at the disk edge (Fig. 3E). Ventral plates have formed on the three proximal arm joints, decreasing in size distalwards on the arm. The lateral plates bear two conical spines each except at the fourth joint, which is just beginning to form and bears a single short spine. The adoral shield spine points outwards and is visible from the dorsal side.

At 1.0 mm dd, the arm consists of eight joints and the terminal plate, although the distal two joints are only just beginning to form. In addition to the primary plates, short radial plates and a large distal and small proximal interradial plate are present (Fig. 3F). Dorsal arm plates are present on three arm joints, the first one oval, the second drop-shaped, and the third triangular. The tooth has grown and a small mouth papilla has formed on the oral plate (Fig. 3G). The oral shields are clearly visible at the disk edge between the adoral shields, but the madreporite is not distinguishable. The first ventral arm plate is elongate-pentagonal, with a convex distal edge and concave lateral edges. Distalwards along the arm this shape is less and less pronounced.

At 1.3 mm dd, a few secondary interradial plates have formed distal to the central primary plate and a k-plate is visible on some radii at the proximal end of the radial shields (Fig. 3H). The first dorsal arm plate is oval, while the others are drop-shaped and separate. On some oral plates, an additional granule-like lateral mouth papilla has formed (Fig. 3I). The adoral shield spine has shortened and a minute papilla has formed on the lateral edge of the first ventral arm plate next to the second tentacle pore, which has moved closer to the mouth slit. The lateral arm plate bears a short, spine-like tentacle scale and proximally three (distally two) spines, about half as long as an arm joint.

At 1.8 mm dd, all k-plates are present and additional interradial plates have formed (Fig. 4A). Three to four genital papillae form the arm comb. The proximal arm joints bear three spines.

At 2.1 mm dd, additional interradial plates have formed (Fig. 4B). There are two to three mouth papillae at each jaw edge, at least one of them on the oral plate; some jaws have one, others two papillae on the dental plate (Fig. 4C). The adoral shield bears two larger papillae and opposite to them the first ventral arm plate bears two smaller papillae, all four pointing at each other across the second tentacle pore. The oral shield has its final, arrow-like shape.

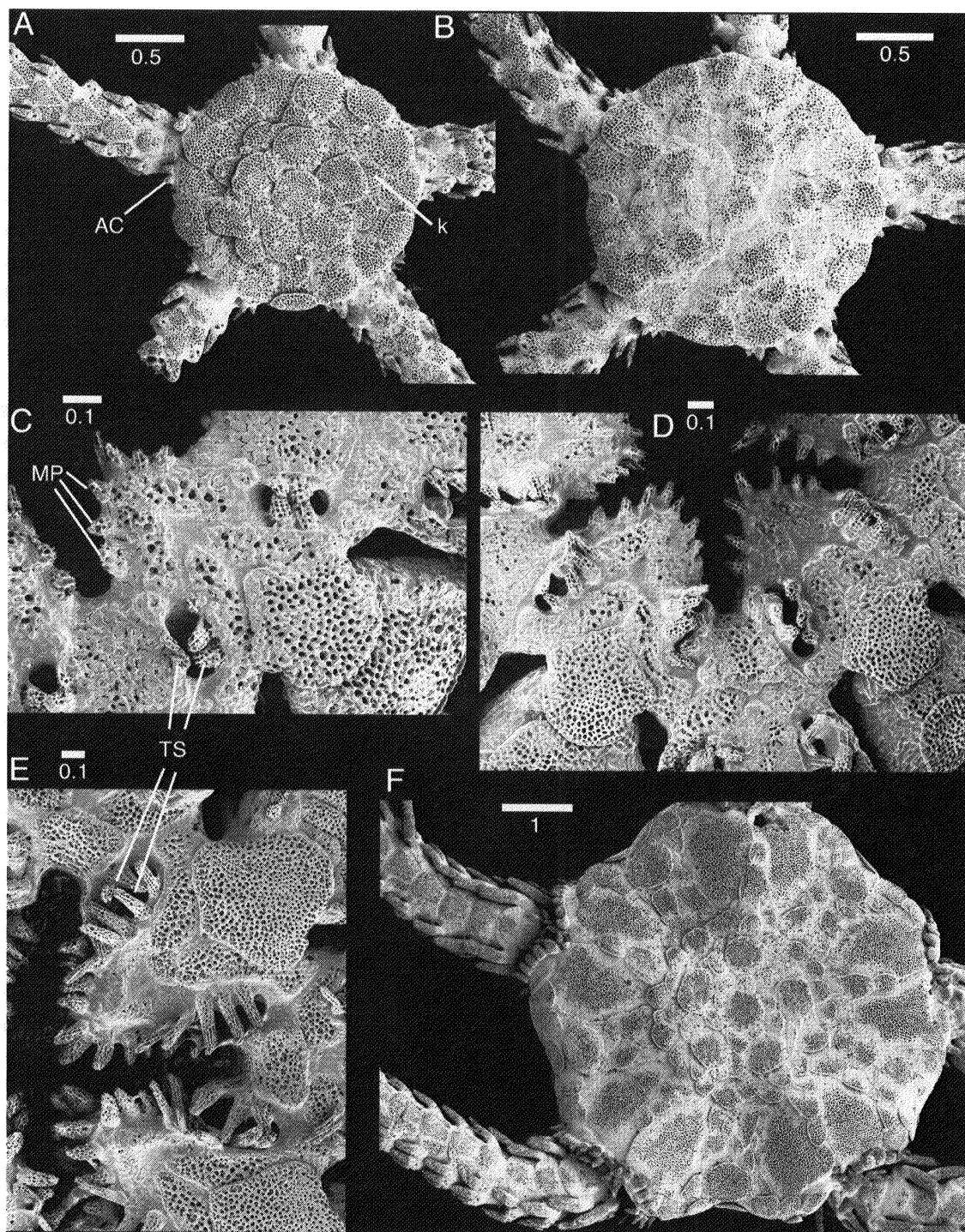


Fig. 4. Continued growth series of *Spinophiura jolliveti* gen. et sp. nov., SEM images, paratypes. A, Postlarva of 1.8 mm dd, SMNH-Type-6056, dorsal aspect; B, C, postlarva of 2.1 mm dd, SMNH-Type-6055, 6053, respectively, dorsal aspect (B) and ventral aspect (C); D, individual of 3.1 mm dd, SMNH-Type-6061, ventral aspect; E, F, individual of 5 mm dd, SMNH-Type-6064, 6065, respectively, ventral aspect (E) and dorsal aspect (F). Abbreviations as in Fig. 2 plus: k, k-plate. Scale bars in millimetres. Type catalogue numbers refer to SEM stubs, not individuals.

The number of disk scales and mouth, tentacle, and genital papillae increases during further growth. At 3.1 mm dd, the second tentacle pore has moved to its final position at the mouth slit, framed by five to six papillae (Fig. 4D). Each jaw edge bears three to four papillae.

At 5 mm dd, the animals show adult characters, although the shape of some skeletal elements still differs from those of the largest adults. In addition to the outer arm comb on the distal genital plate, a short inner comb has formed of a few papillae on the first and second dorsal arm plates (Fig. 4F). These papillae fill the gap between the genital plates and give the appearance of a continuous comb across the arm base. Of the four arm spines on the proximal arm, the dorsalmost is twice as large as the others. The dorsal arm plates are longer than wide on all but the most proximal segments. The mouth papillae have become elongated, spine-like, and more numerous (Fig. 4E). The maximum size observed was 10 mm dd.

Comparisons. The dorsal disk and arms of *S. jolliveti* are similar to those of *Ophiura* species, but the long, spine-like shape of the mouth papillae and tentacle scales is unknown in that genus. Also, the oral shield is rather small compared to that of *Ophiura*. The number of arm spines increases during ontogeny, and since the ontogenetic stage of an individual may be unknown unless complete growth series are available, arm spine number is a character that must be used with caution. The growth series of *S. jolliveti* suggests that the final number of arm spines is five. Many species of *Ophiura* possess three to five arm spines, but these are usually much shorter than an arm joint and appressed (Lyman 1878; Clark 1911, 1915, 1917). The presence of tentacle scales on the first tentacle pore inside the mouth slit has not been described for any other species of ophiuroid, but in the ophiacanthid *Ophiomyces* Lyman, 1869, a scale-like papilla is present at the first tentacle pore, although this is an overlooked and unreported feature (F. Hotchkiss, pers. comm.).

The ontogeny of *S. jolliveti* is similar to that of *Ophiura*, but a buccal scale is absent in the small postlarvae of this species and the first tooth forms quite late during development. In all analyzed species of *Ophiura*, both the first tooth and the buccal scale are present in the earliest stage (Sumida *et al.* 1998; Stöhr 2005). It is unclear which condition is plesiomorphic. The madreporite in the present species cannot be distinguished from the oral shields until almost the adult stage, and all oral shields develop later than in many other species (Sumida *et al.* 1998; Stöhr 2005). During development, some parts of these pentamerous animals develop faster than others, which produces an asymmetrical pattern at some stages, e.g., k-plates on some but not all radii. In particular, the development of the mouth papillae differs between jaws and the final number of papillae in the adult is different on different jaws.

Spinophiura jolliveti shares some characters with *Ophiura* and may be a modified representative of that genus, but the striking differences also merit a taxonomic separation, at the risk of leaving *Ophiura* paraphyletic. We thus propose a new genus, which may be re-evaluated when the relationships of the species and its origin are better understood.

Habitat and distribution. *Spinophiura jolliveti* was found only at vents. The large number of specimens collected (270) suggests that this species is adapted to hydrothermal environments. It is present at several vent sites on the EPR at 9°N (Barbecue, Mussel Bed, East Wall, and Train Station), 13°N (Genesis, Parigo, Julie, and Grandbonum), 17°25'S (Oasis-Rehu), 17°35'S (Wormwood), and 18°36'S (Animal

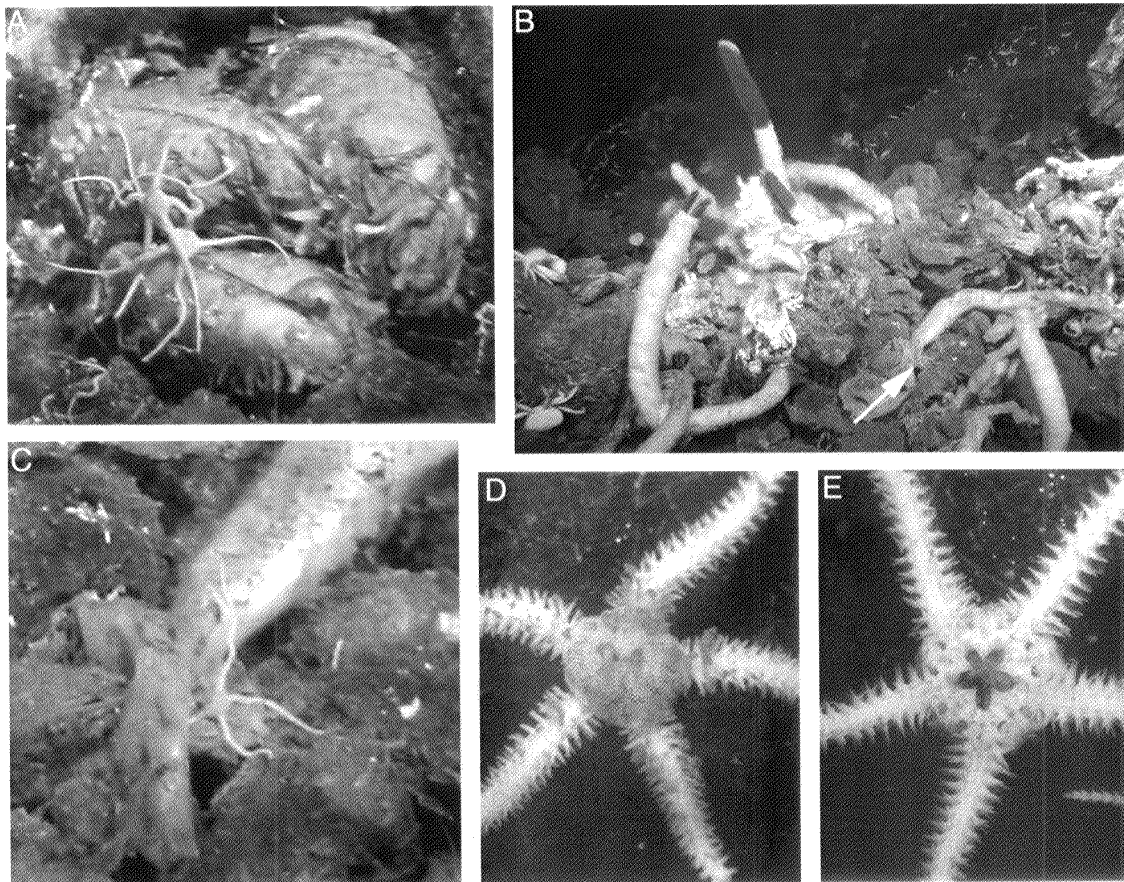


Fig. 5. *Spinophiura jolliveti* gen. et sp. nov. (A–C) and *Ophiolamina eprae* gen. et sp. nov. (D, E). A, Among mussels *Bathymodiolus thermophilus* Kenk and Wilson, 1985, at EPR-13°N, PP-Ph08 hydrothermal vent site; B, giant tube worms *Riftia pachyptila* Jones, 1981 with *S. jolliveti* (arrow), same site; C, close-up detail of B, showing *S. jolliveti* on dead *Riftia*; D, E, live specimen, paratype, MNHN EcOh 20019, about 3.5 mm disk diameter, dorsal aspect (D) and ventral aspect (E), note the orange-red particles adhering to the animal. A–C, Photos from the dive's documentation video (Ifremer/PHARE/N. Le Bris) (A–C) and by Ifremer/PHARE/P. Briand (D, E).

Farm). The structure, abundance, and composition of the animal communities living at these sites are different, but several related invertebrate species are shared by the northern and southern sites (Geistdoerfer *et al.* 1995). *Spinophiura jolliveti* is generally associated with the mytilid bivalve *Bathymodiolus thermophilus* Kenk and Wilson, 1985 (more rarely with the vesicomyid clam *Calypotgena magnifica* Boss and Turner, 1980), living in the hydrothermal fluid where the temperature varies between 2°C and 15°C (Fig. 5A). Large clouds of amphipods were often observed above these mussel beds during the collecting dives. The mussel populations on which these ophiuroids live are sometimes composed of a high number of dead individuals (Van Dover, unpublished data), which may indicate a necrophagous habit. At the northern sites [9°N (Chevaldonné *et al.* 1995) and 13°N], the ophiuroids are found in the same environments as the siboglinid tubeworms *Riftia pachyptila* Jones, 1981 (Fig. 5B, C), crabs *Bythograea thermydron* Williams, 1980,

galatheid crabs *Munidopsis subsquamosa* Henderson, 1885, hippolytid shrimps *Lebbeus* White, 1847, and zoarcid fishes *Thermarces cerberus* Rosenblatt and Cohen, 1986. At the southern sites, these same megafaunal species are present, but in addition, there are holothurians *Chiridota hydrothermica* Smirnov *et al.*, 2000, turrid gastropods *Eosipho auzendei* Warén and Bouchet, 2001, ophiidiid fishes, and high densities of actinostolid sea anemones *Chondrophellia* Carlgren, 1925 and stalked barnacles *Neolepas* Newman, 1979. The relationships between these species and the ophiuroids are not understood yet, but waste products produced by them may provide a food source for the ophiuroids or some species may be predators of ophiuroids.

Family **Ophiacanthidae** s. l. Perrier

Genus **Ophiolamina** gen. nov.

Diagnosis. The type species of up to 3.7 mm dd (possibly growing slightly larger) and five arms of about 15 mm in length. The dorsal disk is covered with low granules, obscuring the disk scales. The radial shields are almost round, about a fifth as long as the dd, and covered with granules. Of the five lateral mouth papillae, the proximal three are lamella-like, extending deep into the mouth slit. The most proximal lamellar papilla is positioned on the dental plate, the other two on the oral plate. The two distalmost papillae are oval and flat, arising from the adoral shield. The madreporite bears a hydropore at a lateral edge. Up to five conical arm spines are present, all erect and as long as an arm joint. Each tentacle pore bears a single large, oval scale.

Etymology. The genus name is composed of *Ophio*, the commonly accepted form for most ophiuroid genera, from Greek “like a snake”, and Latin *lamina* “thin plate, blade, layer”, gender feminine. This name refers to the blade-like mouth papillae of the type species.

Type species. *Ophiolamina eprae* sp. nov.

Description. As for type species.

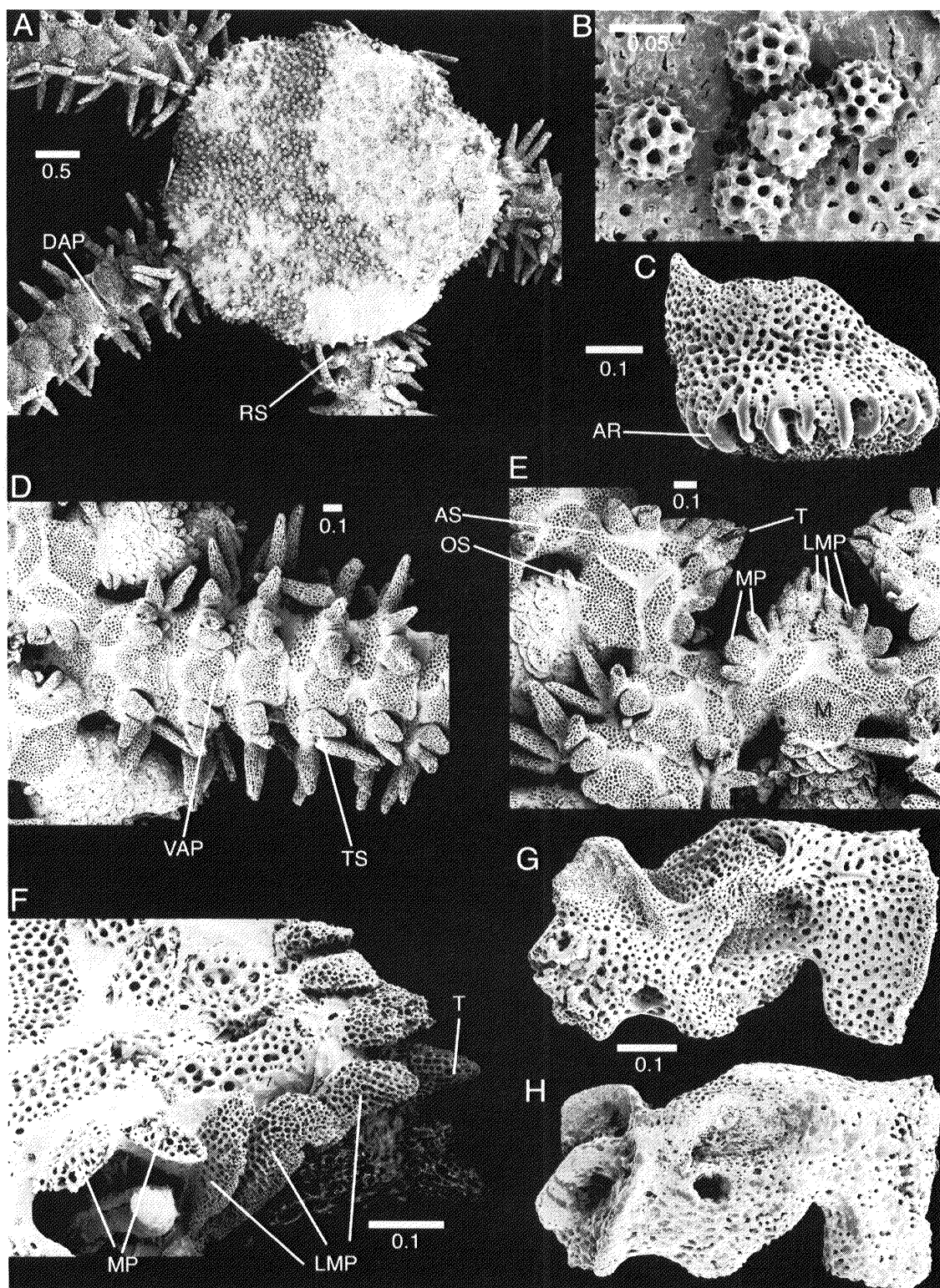
***Ophiolamina eprae* sp. nov.**

(Figs 5D, E, 6–8)

Holotype. 3.7 mm dd, dry, mounted on SEM stub, gold-coated, MNHN EcOs 22637.

Type locality. Cruise PHARE, ROV Victor 6000, dive PL 155, 10 May 2002, slurp gun 2, EPR-13°N, marker PP52, hydrothermal vent site Genesis, 12°48.69'N, 103°56.36'W, 2592 m.

Fig. 6. *Ophiolamina eprae* gen. et sp. nov., SEM images, holotype, MNHN EcOs 22637 (A, B, D–F) and paratypes, MNHN EcOs 22639, 22640 (C, G, H). A, Dorsal aspect; B, disk granules; C, lateral arm plate, showing spine articulation ridges; D, ventral arm; E, mouth, featuring madreporite with lateral hydropore; F, mouth papillae viewed laterally; G, H, oral plate in adradial and abradial aspect, respectively. Abbreviations as in Fig. 2 plus: AR, articulation ridge; LMP, lamellar mouth papillae. Scale bars in millimetres.



Paratypes. Specimens on SEM stubs, gold-coated: 3 spms, BIOSPEEDO, PL 1585, 26 Apr. 2004, SMNH-Type-6108; 2 spms BIOSPEEDO, PL 1590, 1 May 2004, SMNH-Type-6109; 5 spms, SEPR, dive 3349, 8 Feb. 1999, SMNH-Type-6110, 6111; 1 spm, type locality, MNHN EcOs 22638; skeletal elements, type locality, MNHN EcOs 22639, 22640. Specimens in alcohol (80%): 4 spms, type locality, MNHN EcOh 20019; 1 spm, BIOSPEEDO, PL 1579, 19 Apr. 2004, MNHN EcOh 20020; 6 spms (post-larvae), SEPR, dive 3349, sample 5, 8 Feb. 1999, USNM 1078916; 3 spms (postlarvae), SEPR, dive 3349, sample 1, 8 Feb. 1999, USNM 1078918; 1 spm (postlarva), SEPR, dive 3349, sample 4, 8 Feb. 1999, USNM 1078919; 1 spm (postlarva), SEPR, dive 3727, 14 Dec. 2001, USNM 1078920; 2 spms, PAR 5, dive 4097, 31 Mar. 2005, USNM 1078921. For station data see Table 2.

Diagnosis. As for generic diagnosis.

Etymology. The species name is a newly coined word based on the acronym for the type locality EPR (East Pacific Rise). EPR is here regarded as feminine.

Description of holotype. The disk measures 3.7 mm in diameter. All five arms are broken, but at least four times longer than dd. The dorsal disk is covered by small, round, imbricating scales and larger, almost round, radial shields, all of which are obscured by low, slightly rough granules (partly abraded; Fig. 6A, B). The disk is slightly incised interradially. The pairs of radial shields are each separate along their distal half. The arms are not particularly noded; there are five erect arm spines on the proximal segments, tapered, smooth, and about as long as an arm joint. The dorsal arm plate is fan-shaped, plates on neighbouring joints just touching. On the distal part of the arm, the dorsal plates are widely separated by the large lateral plates, and the three short arm spines bear thorny ridges along their length. The arm spine articulation is formed by two parallel ridges (Fig. 6C).

The ventral disk is formed of numerous small, round, overlapping scales bearing scattered granules similar to those of the dorsal side. The first ventral arm plate is smaller than the others, located almost completely inside the mouth slit (Fig. 6D). The other ventral arm plates are pentagonal with an obtuse proximal angle, concave lateral edges, and slightly concave distal edge. Neighbouring plates are separate. Each tentacle pore is covered by a large, oval to leaf-shaped scale. The adoral shields have curved, concave proximal edges and extend around the lateral angle of the oral shield, separating it from the lateral arm plates. The oral shield is wider than long with an obtuse proximal angle and a convex distal edge bearing one to several granules similar to the disk granules. The madreporite bears a large hydropore at a lateral edge (left in oral view). The dental plate bears conical, pointed teeth on its proximal surface and a lateral, blade-like papilla on either side, all of which almost meet (Fig. 6E). On three jaws a small papilla is present on the ventral edge of the dental plate, between the lateral blades. Each oral

Fig. 7. Growth series of *Ophiolamina eprae* gen. et sp. nov., SEM images, paratypes. A, B, Postlarva of 0.7 mm dd, SMNH-Type 6111, dorsal aspect (A) and ventral aspect, with glue residue obscuring plates (B); C, D, postlarva of 0.8 mm dd, SMNH-Type- 6110, dorsal aspect (C) and mouth (D); E, F, postlarva of 1.0 mm dd, SMNH-Type-6108, dorsal aspect (E) and ventral aspect (F); G, H, postlarva of 1.2 mm dd, SMNH-Type-6111, dorsal aspect (G) and ventral aspect (H). Abbreviations as in Figs 2–4 plus: BS, buccal scale; LAP, lateral arm plate. Scale bars in millimetres. Type catalogue numbers refer to SEM stubs, not individuals.

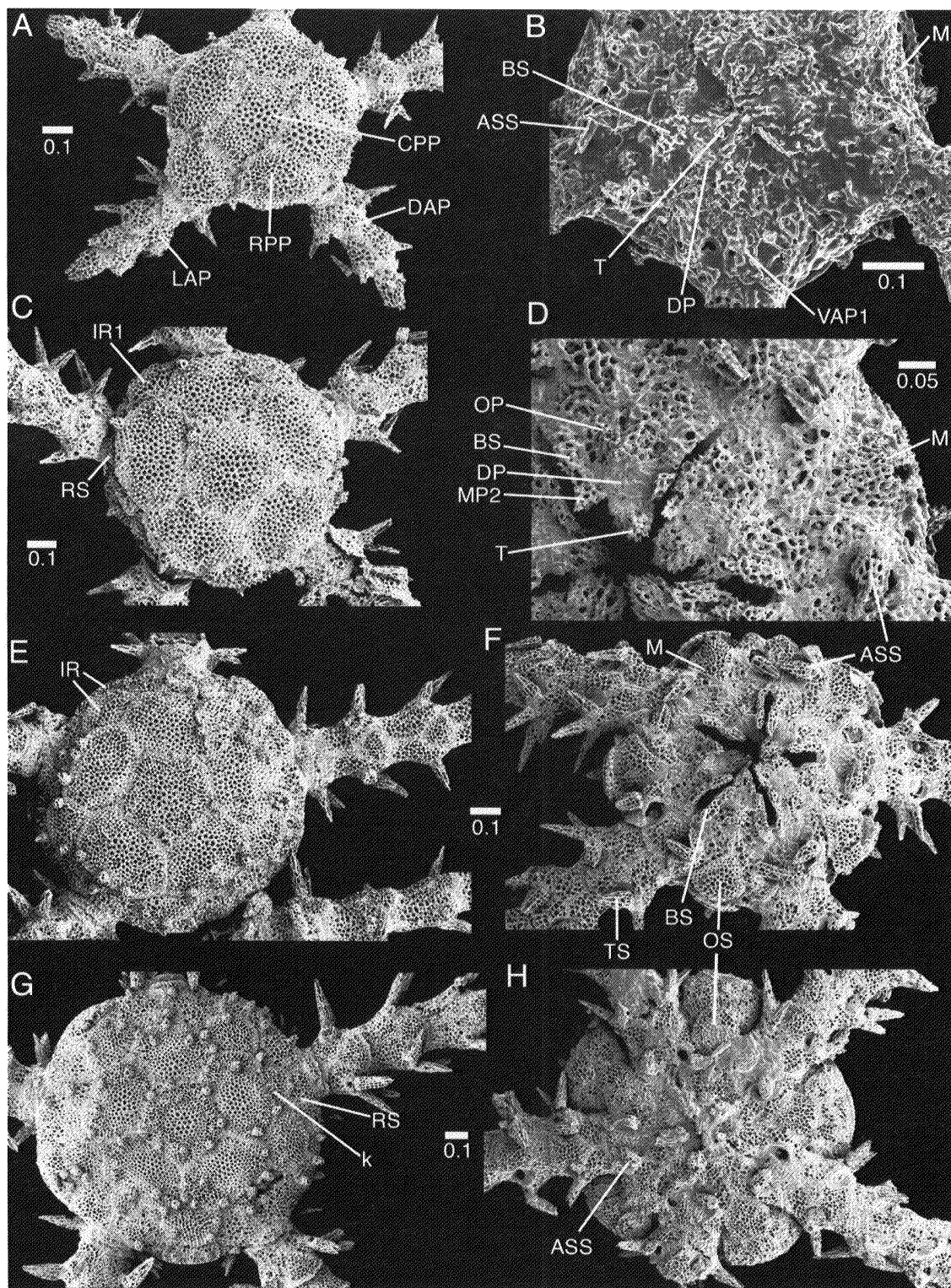


plate bears two similar blade-like lateral papillae, all of which extend almost vertically into the mouth slit (Fig. 6F). The edge of the adoral shield next to the second tentacle pore bears two scale-like papillae, which continue the row of mouth papillae (Fig. 6E).

The coloration of this species in life is a light pinkish orange to cream.

Paratype variation. Oral plates were dissected from a smaller paratype to save the holotype. The oral plate is of an elongated axe-shape with small muscle attachment scars (Fig. 6G, H).

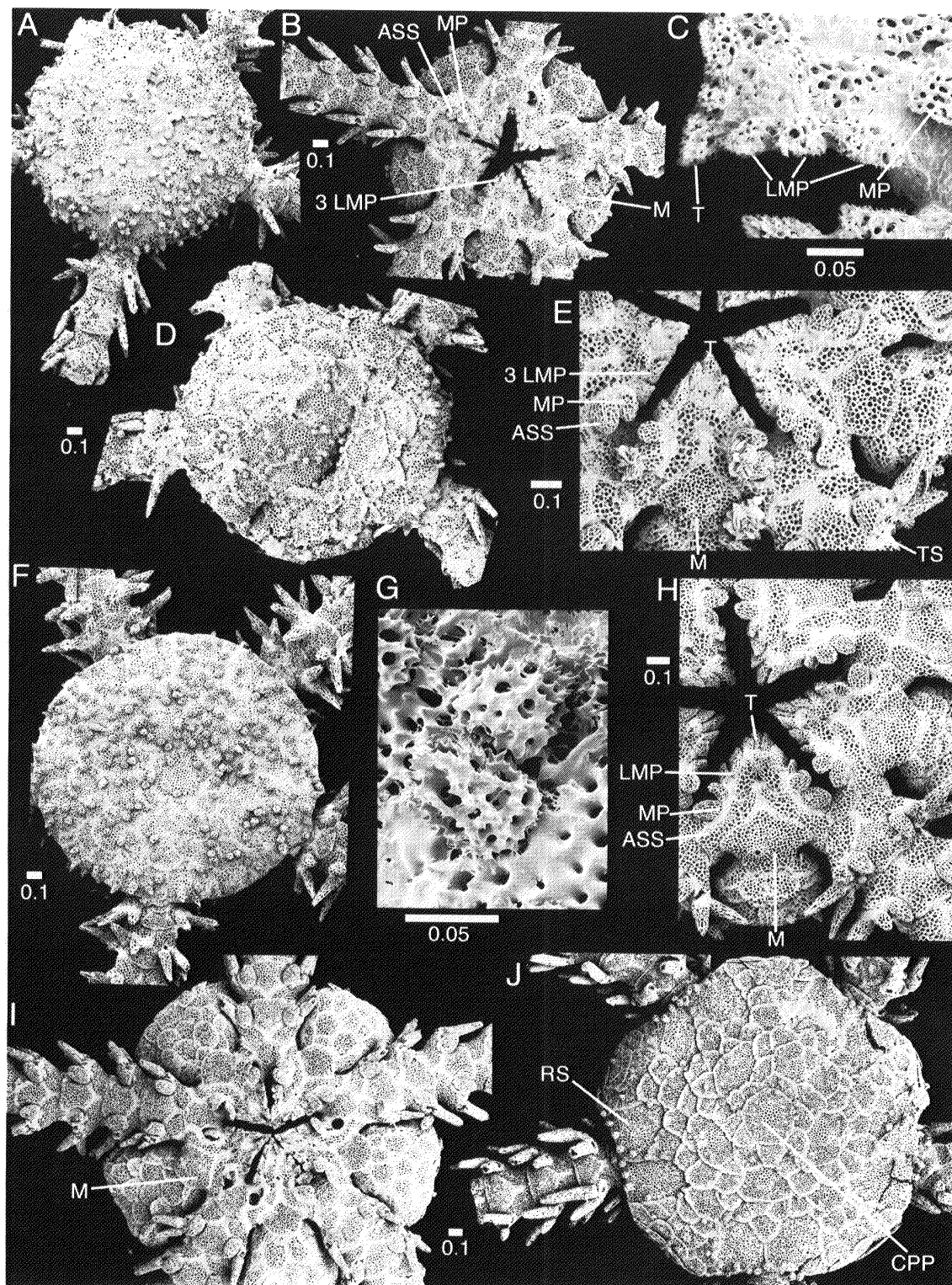
Most of the collected specimens are rather small juveniles, the holotype being the largest adult. The largest paratype measures 3.5 mm dd. Its hydropore is more on top of the madreporite than in the holotype. The next smaller paratype, at 3.1 mm dd, has no visible hydropore at all, while smaller individuals have visible hydropores. The disk granules are abraded to varying extents, leaving parts of the disk naked. The number of granules on the edge of the oral shields varies both between jaws and between individuals. Apart from this, variation is related to ontogenetic stage, as described below. The animals are often covered with bright orange-red mineral particles, which are also found in their mouth and stomach (Fig. 5D, E).

Postmetamorphic development (paratypes). The smallest postlarva found measures 0.7 mm dd; its arms have three joints and a tapered terminal plate (Fig. 7A). The dorsal disk is formed by the central primary plates and six instead of the usual five radial primary plates, which is probably an aberration. A few conical granules are scattered across the disk. The plate structure is multilayered with larger fenestrations in the centre of the plates and a rough surface. The radial shields have just begun to form distal to the radial primary plates. Each lateral arm plate bears two pointed, thorny spines and the proximal segment bears a small, triangular dorsal plate. The jaw bears a large, pointed tooth on the small dental plate and a wide buccal scale (=first mouth papilla) on the oral plate (Fig. 7B). The adoral shield bears a short, conical spine. The oral shields are visible at the disk edge, the madreporite having a projecting hydropore (not figured).

At 0.8 mm dd the first interradiial plates are present (Fig. 7C). This individual has only five primary radial plates, confirming the above assumption that six plates is not the typical pattern. The dental plate bears a wide tooth and a short secondary papilla to either side (Fig. 7D). The adoral shield spine is flattened and points across the second tentacle pore. The oral shields are drop-shaped. The madreporite bears a conical protrusion with a large hydropore opening. Ventral arm plates are present on three joints, about twice as long as wide, with concave lateral edges, a narrow proximal angle, and a wider, convex distal edge.

At 1.0 mm dd there are two interradiial plates, a proximal and a distal one of equal size, but it is unclear which of them formed first (Fig. 7E). The fan-shaped

Fig. 8. Continued growth series of *Ophiolamina eprae* gen. et sp. nov., SEM images, paratypes. A–C, Postlarva of 1.4 mm dd, SMNH-Type-6108, dorsal aspect (A), ventral aspect (B), and mouth papillae (C); D, E, postlarva of 1.6 mm dd, SMNH-Type-6108, dorsal aspect (D) and ventral aspect (E); F–H, postlarva of 2.0 mm dd, MNHN EcOs 22638, dorsal aspect (F), disk granules (G), and ventral aspect (H); I, J, individual of 2.3 mm dd, SMNH-Type-6109, ventral aspect (I) and dorsal aspect (J). Abbreviations as in Figs 2, 3, 6. Scale bars in millimetres. Type catalogue numbers refer to SEM stubs, not individuals.



dorsal arm plates are widely separated by the long lateral plates. The still projecting hydropore is slightly off-centre on the madreporite; the mouth papilla on the dental plate has become wider and slanting, with its distal end deeper than its proximal end (Fig. 7F). The buccal scale is unchanged. A large, flat adoral shield spine covers the second tentacle pore (on one plate there are two spines). A large, oval, flat scale covers each tentacle pore on the arm.

At 1.2 mm dd the rounded wedge-shaped k-plate has formed between the proximal ends of the radial shields and the number of granules on the disk has increased (Fig. 7G). Of the first dorsal arm plate, only the distal edge is visible beneath the radial shields. A row of three round scales forms the ventral disk (Fig. 7H). The second tentacle pore has moved closer to the mouth slit. The number of mouth papillae is unchanged. The bursal slits have formed.

At 1.4 mm dd additional interrarial plates have formed and the number of granules has increased (Fig. 8A). Each lateral arm plate bears three equal spines. On some jaw edges a third mouth papilla has formed on the proximal part of the oral plate, between the second papilla and the buccal scale (Fig. 8B). On other jaw edges, the buccal scale is still as wide as the entire oral plate, which suggests that the third papilla forms by division of the buccal scale. Both proximal papillae are beginning to attain the blade-like shape and orientation of the adult (Fig. 8C). The adoral shield bears two flat, oval scales, the proximal one being smaller than the distal one, which suggests that the proximal one has formed secondarily and that the distal scale is the adoral shield spine. The hydropore is now almost on the same level as the plate surface, moved to the lateral part of the madreporite.

At 1.6 mm dd numerous additional scales have formed on the dorsal disk (Fig. 8D). The three mouth papillae have attained their blade-like shape and the scales on the adoral shield form a row continuous with them (Fig. 8E). The oral shields are about as wide as long.

At 2.0 mm dd each lateral arm plate bears four equal, tapered spines (Fig. 8G). The disk granules are thorny and higher than wide (Fig. 8H). The oral shields have become wider than long (Fig. 8I).

At 2.3 mm dd the animals can be identified using adult characteristics (Fig. 8J, K). The hydropore has not yet reached its final position at the edge of the madreporite, but the proximal three mouth papillae have a pronounced blade-like shape and a vertical orientation.

Comparisons. The Ophiacanthidae include a wide variety of genera and species, many of which are ill-defined and in great need of revision (O'Hara and Stöhr in press). The current diagnosis of the family includes a wide range of character states, such as a disk covered more or less with spinelets, granules, or rods of varying size and shape, more or less noded arms, and thorny or smooth arm spines (Paterson 1985). With such a wide definition, it is difficult to decide whether a species belongs in this family or not. The granulated disk, the position of the second tentacle pore inside the mouth slit, the interradially incised disk, and the large tentacle scale of the new species fit within the definition of the Ophiacanthidae. Various skeletal elements have been suggested as characteristic of certain taxa, but few have been confirmed to have family-specific taxonomic value. Paterson (1985) suggested that a comma-shaped arm spine articulation might be specific for most Ophiacanthidae, excepting his subfamily Ophiohelinae, which includes species with a sac-like disk that probably lacks radial shields. Recently, several

species of Ophiacanthidae not belonging to the Ophiotominae have been shown also to lack a comma-shaped articulation (Stöhr and Segonzac 2005; O'Hara and Stöhr in press), which brings into question the taxonomic value of this character. Murakami (1963) described the oral plates of a large number of species from most families of ophiuroids and showed them to be family-specific. According to that work, the oblong axe-like shape of the oral plate with rather small adradial and abradial muscle attachment scars places *Ophiolamina eprae* within the Ophiacanthidae.

The present new species shows affinities with several of the subfamilies of Ophiacanthidae proposed by Paterson (1985). The elongate adoral shields are similar to those of the Ophiotominae and the flat, round distal mouth papillae resemble those of the ophiotomine *Ophiolimna* Verrill, 1899, but the jaw is not elongate and the second tentacle pore is not superficial as is typical for that subfamily (Paterson 1985). The short, round radial shields, the disk granules, and the shape and structure of the arms resemble those of *Ophiomitrella* in the subfamily Ophioplinthacinae, but that genus has short adoral shields. Among the Ophioplinthacinae, some species of *Ophiocamax* Lyman, 1878 possess long adoral shields (Paterson 1985) but are otherwise different from the new species, which nonetheless may perhaps belong to this subfamily. The delimitation of the ophiacanthid subfamilies needs further examination, as is exemplified by the recent removal of *Ophiomelina* Koehler, 1922 from the Ophioplinthacinae by its synonymisation with *Ophiacantha* Müller and Troschel, 1842, which belongs to the subfamily Ophiacanthacinae (O'Hara and Stöhr in press). While *O. eprae* clearly belongs within the Ophiacanthidae, placing it within a subfamily would only add to the existing confusion.

The blade-like proximal mouth papillae are unique for this species among all ophiuroids and bear some similarity to the mouth papillae of *Ophioctenella acies*, because they may superficially be mistaken for a single wide papilla along the jaw edge when viewed from the oral side.

Habitat and distribution. *Ophiolamina eprae* was collected at 13°N (Grand-bonum site), in the hydrothermal sediment on the walls of a sulphide edifice colonized by some siboglinid tubeworms *Riftia pachyptila* and galatheid crabs *Munidopsis subsquamosa*, and at the Julie site, around a hydrothermal fluid emission (13 to 18°C) with some *R. pachyptila* and mussels and associated bythograeid crabs and hippolytid shrimps. The ophiuroids were preferentially associated with the mussels, but some were collected with empty tubes of *R. pachyptila*.

Discussion

Four species of ophiuroid are now known from chemosynthetically based environments, two each of the families Ophiuridae and Ophiacanthidae. Among the previously described species, *Ophienigma spinilimbatus* is restricted to seeps, while *Ophioctenella acies* occurs at both vents and seeps and has a wide distribution across the Atlantic Ocean (Stöhr and Segonzac 2005). Both new species described herein appear to be restricted to vents. So far, none of these species has been found in more than one ocean.

The geographic distribution of the ophiacanthid *Ophiolamina eprae* as known at present is discontinuous, with a large gap between the type locality at 12°48'N and its southern area of occurrence. Its population densities in samples are much

lower than those of the ophiurid *Spinophiura jolliveti* except at Animal Farm (SEPR, 18°36'S), but this may also reflect poor collecting results. Ophiacanthidae are generally known to have a cryptic life-style, hiding in crevices and often epizoic on coral and other animals, which may make them more difficult to collect. The largest numbers of individuals of *Ophiolamina eprae* (small juveniles) were collected by the quantitative pot method employed by the SEPR cruise in 1999 at Animal Farm. Both ophiuroid species have been collected from mussel beds and aggregations of tubeworms, two phylogenetically widely separate taxa. The ophiuroids may find shelter among the shells and tubes and perhaps feed on bacterial mats or waste products generated by both mussels and worms. *Ophiolamina eprae* seems attracted to decaying organic material, since its greatest numbers were found at the Animal Farm vent field, in a dying mussel community with no hydrothermal activity (Van Dover, pers. comm.). Densities of both species were far lower than those of *Ophioctenella acies* of MAR vents, which reaches densities up to 80 ind. dm⁻² at some sites (Gebruk *et al.* 2000), but perhaps the most favourable sites for the two new species have not been found yet. At Animal Farm (18°36'S), *Spinophiura jolliveti* was collected in 1999 (SEPR cruise) and 2004 (BIOSPEEDO), and at the Oasis-Rehu site, in 1993 (NAUDUR), 1999 (SEPR), and 2004 (BIOSPEEDO), which indicates a certain temporal stability of the environmental conditions favourable to this species. The two new species occur in sympatry at some sites (Animal Farm, Rehu), but not enough is known about their adaptations and life-style to understand the ecological relationships between the species.

The presence of juveniles of different age classes suggests several previous recruitment events, instead of occasional random settling. This is a strong indication that both species are adapted to the vent environment. *Spinophiura jolliveti* settles at an early postmetamorphic stage with arms consisting of only the terminal plate, and at 0.4 mm disk diameter it is one of the smallest bottom-living stages known (Sumida *et al.* 1998; Stöhr 2005). The larger postlarva of *Ophiolamina eprae* may suggest later settlement or abbreviated development, although the smallest stage may not have been found yet. Nothing is known about the function of the mouth papillae in ophiuroids. The great diversity in their shape, size, and number suggests that they are not just for closing the mouth gap, but somehow assist in feeding. The blade-like proximal papillae of *Ophiolamina eprae* may perhaps function as scrapers of bacterial mats, or for grinding up dead tissue if the species is a scavenger.

Acknowledgements

The authors thank the chief scientists (see Table 1) and crews of R/V *L'Atalante Nadir*, *Vickers*, and *Natsushima*, of D/S *Nautille*, *Alvin*, and *Shinkai 2000*, and of ROV *Victor 6000*, for collecting all the specimens studied here, and most particularly Didier Jollivet, CNRS, Roscoff (BIOSPEEDO) and Nadine Le Bris, Ifremer, Brest (PHARE). The BIOSPEEDO and PHARE cruises were funded by CNRS and Ifremer, on the framework of the two thematic workshops DORSALES and Ecchis GDR. We thank N. Le Bris and P. Briand (Ifremer, Brest) for supplying the colour photos. We also thank B. Govenar (Pennsylvania State University, USA), R. Vrijenhoek (MBARI, California), and C. Van Dover (College of William and Mary, USA),

for donating their samples. Many thanks also to C. Van Dover and two anonymous referees for valuable suggestions to improve the manuscript. The *Alvin/Atlantis* programs were funded by grants from the U.S. National Science Foundation to R. C. Vrijenhoek (OCE-0241613) and C. L. Van Dover (OCE-0350554). This study was supported by a grant from Riksmusei Vänner, Stockholm, to S. Stöhr.

References

- Chevaldonné, P., Godfroy, A., Guézennec, J., Lesongeur, F., Fouquet, Y., Barbier, G. and Desbruyères, D. 1995. Preliminary description of the micro-scale ecology of a hydrothermal vent chimney at 9°50'N on the East Pacific Rise. *InterRidge* 4: 18–20.
- Clark, H. L. 1911. North Pacific ophiurans in the collection of the United States National Museum. *United States National Museum Bulletin* 75: 1–302.
- Clark, H. L. 1915. Catalogue of recent ophiurans: based on the collection of the Museum of Comparative Zoology. *Memoirs of the Museum of Comparative Zoology at Harvard College* 25: 165–376.
- Clark, H. L. 1917. Reports on the scientific results of the Albatross Expedition to the tropical Pacific, 1899–1900 (Part 18). Reports on the scientific results of the Albatross Expedition to the eastern tropical Pacific, 1904–1905 (Part 30). Ophiuroidea. *Bulletin of the Museum of Comparative Zoology at Harvard College* 61: 428–453.
- Gage, J. D. and Tyler, P. A. 1991. *Deep-Sea Biology: a Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge, xvi+504 pp.
- Gebruk, A. V., Chevaldonné, P., Shank, T., Lutz, R. A. and Vrijenhoek, R. C. 2000. Deep-sea hydrothermal vent communities of the Logatchev area (14°45'N, Mid-Atlantic Ridge): diverse biotopes and high biomass. *Journal of the Marine Biological Association of the United Kingdom* 80: 383–393.
- Geistdoerfer, P., Auzende, J.-M., Ballu, V., Batiza, R., Bideau, D., Cormier, M.-H., Fouquet, Y., Lagabrielle, Y., Sinton, J. and Spadea, P. 1995. Hydrothermalisme et communautés animales associées sur la dorsale du Pacifique Est entre 17° et 19°S (campagne NAUDUR). *Comptes Rendus de l'Académie des Sciences. Série II, Sciences de la Terre et des Planètes* 320: 47–54.
- Halanych, K. M., Tieger, M., O'Mullan, G. D., Lutz, R. A. and Vrijenhoek, R. C. 1999. Brief description of biological communities at 7°S on the Eastern Pacific Rise. *InterRidge* 8: 23–27.
- Hecker, B. 1985. Fauna from a cold sulfur-seep in the Gulf of Mexico: comparison with hydrothermal vent communities and evolutionary implications. *Bulletin of the Biological Society of Washington* 6: 465–473.
- O'Hara, T. D. and Stöhr, S. In press. Deep water ophiuroids of New Caledonia: Ophiacanthidae and Hemieuryalidae. *Tropical Deep Sea Benthos*.
- Lyman, T. 1878. Ophiuridae and Astrophytidae of the «Challenger» expedition. Part I. *Bulletin of the Museum of Comparative Zoology at Harvard College* 5: 65–168.
- Murakami, S. 1963. The dental and oral plates of Ophiuroidea. *Transactions of the Royal Society of New Zealand, Zoology* 4: 1–48.
- Paterson, G. L. J. 1985. The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History), Zoology Series* 49: 1–162.
- Sibuet, M. and Olu, K. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research II* 45: 517–567.

- Smith, A. B., Paterson, G. L. J. and Lafay, B. 1995. Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives. *Zoological Journal of the Linnean Society* 114: 213–243.
- Smith, C. R., Baco, A. R. and Glover, A. G. 2002. Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. *Cahiers de Biologie Marine* 43: 293–297.
- Stöhr, S. 2005. Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society* 143: 543–576.
- Stöhr, S. and Segonzac, M. 2005. Deep-sea ophiuroids (Echinodermata) from reducing and non-reducing environments in the North Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom* 85: 383–402.
- Sumida, P. Y. G., Tyler, P. A., Gage, J. D. and Nørrevang, A. 1998. Postlarval development in shallow and deep-sea ophiuroids (Echinodermata: Ophiuroidea) of the NE Atlantic Ocean. *Zoological Journal of the Linnean Society* 124: 267–300.
- Tyler, P. A., German, C. R., Ramirez-Llodra, E. and Van Dover, C. 2003. Understanding the biogeography of chemosynthetic ecosystems. *Oceanologica Acta* 25: 227–241.
- Tyler, P. A., Paterson, G. J. L., Sibuet, M., Guille, A., Murtons, B. J. and Segonzac, M. 1995. A new genus of ophiuroid (Echinodermata: Ophiuroidea) from hydrothermal mounds along the Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the United Kingdom* 75: 977–986.
- Van Dover, C. L. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295: 1253–1257.